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PROPULSION BY HISPID FLAGELLA

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INTRODUCTION

When a smooth flagellum propels a freely swimming organism, the movement of the organism is in the opposite direction to the propagation of flagellar waves, while a flagellum bearing projections which remain perpendicular to the flagellar surface during movement may produce a propulsive force in the direction of the propagated wave. A qualitative explanation of the phenomenon of reversal of the direction of propulsion by flagella bearing mastigonemes has been given by Jahn, Landman & Fonseca (1964), but a theoretical treatment of the situation has not yet been published explicitly; Taylor (1952) has presented a mathematical analysis of a related system.

In the present paper surface coefficients of resistance as first used in connexion with flagellar propulsion by Gray & Hancock (1955) will be employed to derive expressions for the propulsive velocities of organisms propelled by sinusoidally and helically undulating hispid flagella. Some experimental results will be presented to test the equations obtained.

THEORY

In the theoretical evaluation of the forces involved in propulsion by smooth flagella Gray & Hancock (1955) made use of surface coefficients of resistance C_N and C_T, which are respectively the forces acting normal to and parallel to the axis of a cylinder of unit length moving with unit velocity along the line of action of the forces. For a smooth cylinder of radius r and length l moving in a fluid of viscosity μ it has been shown that

$$C_T = \frac{2\pi\mu}{\ln(2l/r) - \frac{1}{2}}. \tag{1}$$

and

$$C_N = 2C_T \tag{2}$$

(Hancock, 1953; Gray & Hancock, 1955).

In the work of Gray & Hancock the equality of equation (1) was introduced at an early stage, thus producing equations containing C_T only which indicated that an isolated filament along which was propagated a sinusoidal wave would move in the direction opposite to that of the wave motion. Similar equations have been developed

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for helical waves by Holwill & Burge (1963). The surface coefficients of force for a rough cylinder will not be related in the manner indicated by equation (2).

Propulsion by undulating filaments

In the analysis of propulsion by undulating rough cylinders the basic mathematics of the argument remains the same as for smooth cylinders, but the coefficients C_N and C_T must be retained separately throughout. To evaluate the force produced by a filament executing a sinusoidal wave motion, the force dF exerted by a small element of the filament is first calculated, and an integration over the whole length of the filament then performed. The force dF is given by equation (xiv) of Gray & Hancock (1955):

$$dF = \frac{\left\{(C_N - C_T)\frac{dy}{dt}\frac{dy}{dx} - u\left[C_T + C_N\left(\frac{dy}{dx}\right)^2\right]\right\}}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{\frac{1}{2}}}, \tag{3}$$

where u is the average propulsive velocity of the filament in the x-direction.

For a sine wave whose equation is

$$y = \eta \sin \frac{2\pi}{\lambda}(x + V_w t),$$

where η, λ are the amplitude and wavelength of the wave and V_w is the wave velocity,

$$\frac{dy}{dx} = \frac{2\pi\eta}{\lambda} \cos \frac{2\pi}{\lambda}(x + V_w t),$$

and

$$\frac{dy}{dt} = \frac{2\pi V_w \eta}{\lambda} \cos \frac{2\pi}{\lambda}(x + V_w t).$$

Making use of these relations and putting $dy/dx = A$, equation (3) becomes

$$dF = \frac{(C_N - C_T)V_w A^2 + u(C_T + C_N A^2)}{(1 + A^2)^{\frac{1}{2}}} dx. \tag{4}$$

The force generated by a complete wave is

$$F = \int_0^\lambda dF = (C_N - C_T)V_w \int_0^\lambda \frac{A^2}{(1 + A^2)^{\frac{1}{2}}} dx - uC_N \int_0^\lambda \frac{[C_T/C_N] + A^2}{(1 + A^2)^{\frac{1}{2}}} dx. \tag{5}$$

By neglecting the contribution to the integrals of the term in $\cos(4\pi/\lambda)(x + V_w t)$ it can be shown that, approximately

$$\int_0^\lambda \frac{A^2}{(1 + A^2)^{\frac{1}{2}}} dx = \frac{\frac{1}{2}\eta^2 k^2}{(1 + \eta^2 k^2)^{\frac{1}{2}}} \lambda \tag{6}$$

and

$$\int_0^\lambda \frac{[C_T/C_N] + A^2}{(1 + A^2)^{\frac{1}{2}}} dx = \frac{[C_T/C_N] + \frac{1}{2}\eta^2 k^2}{(1 + \frac{1}{2}\eta^2 k^2)^{\frac{1}{2}}} \lambda, \tag{7}$$

where $k = 2\pi/\lambda$, so that

$$F = (C_N - C_T)V_w\lambda \frac{\frac{1}{2}\eta^2k^2}{(1+\frac{1}{2}\eta^2k^2)^{\frac{1}{2}}} - uC_N\lambda\frac{[C_T/C_N]+\frac{1}{2}\eta^2k^2}{1+\frac{1}{2}\eta^2k^2}. \tag{8}$$

For an isolated filament $F = 0$, and then

$$\frac{u}{V_w} = \frac{(1-[C_T/C_N])\,\frac{1}{2}\eta^2k^2}{[C_T/C_N]+\frac{1}{2}\eta^2k^2}. \tag{9}$$

For small ηk, equation (9) reduces to

$$\frac{u}{V_W} = \left(\frac{C_N - C_T}{C_T}\right)\frac{\eta^2k^2}{2} \tag{10}$$

an equation obtained by Howland (cited in Gray & Hancock, 1955).

If the filament is propelling an inert head, $F = C_Hua$ where C_H is the drag coefficient of the head and a is a linear dimension; for a spherical head, $C_H = 6\pi\mu$. Making the appropriate substitution we obtain

$$\frac{u}{V_w} = \frac{\eta^2k^2(1-[C_T/C_N])}{[2aC_H/n\lambda C_N](1+\frac{1}{2}\eta^2k^2)^{\frac{1}{2}}+[2C_T/C_N]+\eta^2k^2}, \tag{11}$$

where n is the number of wavelengths contained by the filament.

Similar analyses for helical waves show that for an isolated filament

$$\frac{u}{V_w} = \frac{\eta^2k^2(1-[C_T/C_N])}{\eta^2k^2+[C_T/C_N]}, \tag{12}$$

and for a filament propelling an inert head

$$\frac{u}{V_w} = \frac{2\eta^2k^2(1-[C_T/C_N])}{[2aC_H/n\lambda C_N](1+\eta^2k^2)^{\frac{1}{2}}+[2C_T/C_N]+2\eta^2k^2}. \tag{13}$$

From equations (9) and (11)–(13) it is clear that the sign of u/V_w depends on the magnitude of the ratio C_T/C_N. If $C_T/C_N < 1$, as in the case of smooth flagella u/V_w is positive, so that u and V_w are in *opposite* directions, while if $C_T/C_N > 1$, u/V_w is negative and u will be in the same direction as V_w. The form of equation (9) is illustrated in Fig. 1, where values of u/V_w are plotted against ηk for values of C_T/C_N in the range 1–2. The curve corresponding to a smooth flagellum ($C_T/C_N = 0{\cdot}5$) is included for purposes of comparison, although it must be remembered that in this case (u/V_w) is positive.

Power dissipation

The rate of working δP of a filamant of length δs along which is passing an undulatory wave is the product of the force and velocity and is given by

$$\delta P = (C_NV_N^2 + C_TV_T^2)\delta s. \tag{14}$$

For a sinusoidal wave, $ds = [1+(dy/dx)^2]^{\frac{1}{2}}dx$.

Making the appropriate substitutions and integrating we obtain

$$\frac{P}{V_w^2} = \frac{1}{2}\frac{\eta^2k^2\lambda C_N}{(1+\frac{1}{2}\eta^2k^2)^{\frac{1}{2}}}\left(\frac{u}{V_w}-1\right)^2 + \frac{\lambda C_T}{(1+\frac{1}{2}\eta^2k^2)^{\frac{1}{2}}}\left[\frac{1}{4}\eta^4k^4 + \frac{u}{V_w}\eta^2k^2 + \frac{u^2}{V_w^2}\right], \tag{15}$$

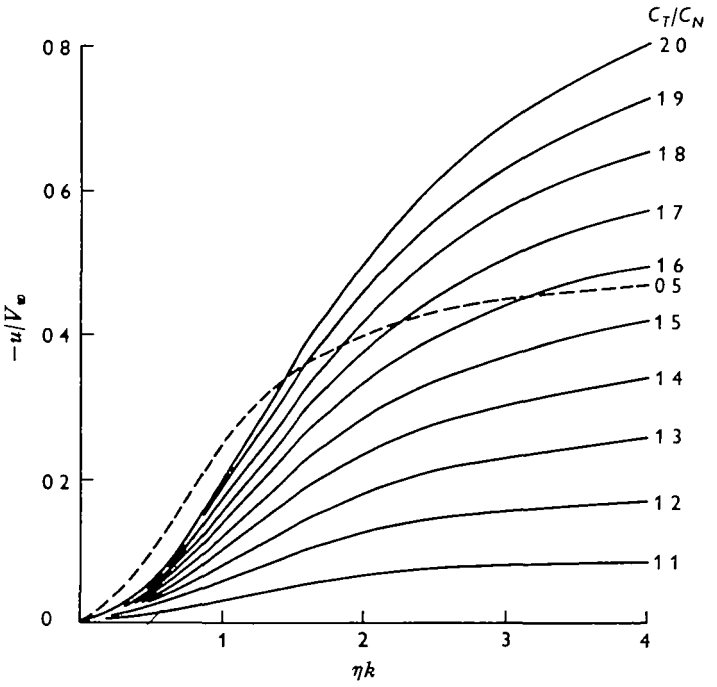

Fig. 1. Variation of u/V_w with ηk at various values for C_T/C_N for an isolated filament executing sinusoidal waves. For the curve $C_T/C_N = 0{\cdot}5$, u/V_w must be taken as positive.

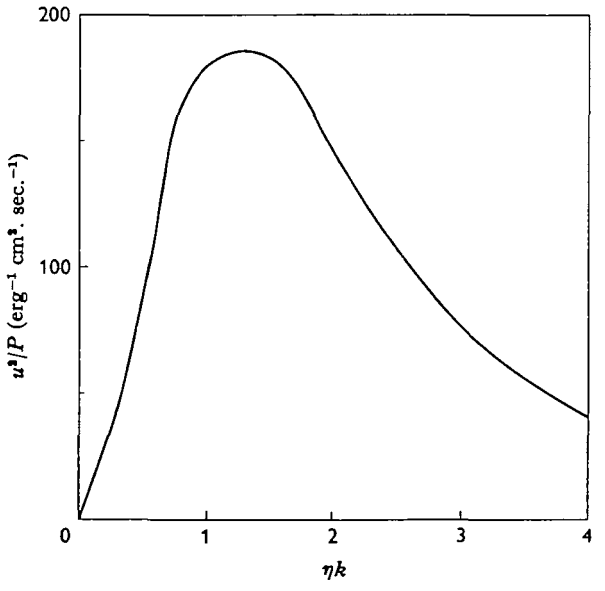

Fig. 2. Variation of u^3/P with ηk for a filament executing sinusoidal waves.

where u/V_w is given by equation (9). A similar expression holds for a filament executing helical waves. A graph of u^2/P (a measure of the propulsive efficiency of a flagellum) against ηk is shown in Fig. 2. for a flagellum whose characteristics are similar to those described in a later section of this paper (see p. 272).

Evaluation of surface coefficients for rough cylinders

To be of practical application in the field of flagellar motion, the type of roughness to be considered consists of thin cylindrical projections (representing mastigonemes) perpendicular to the axis of the main cylinder (representing the flagellum). Several

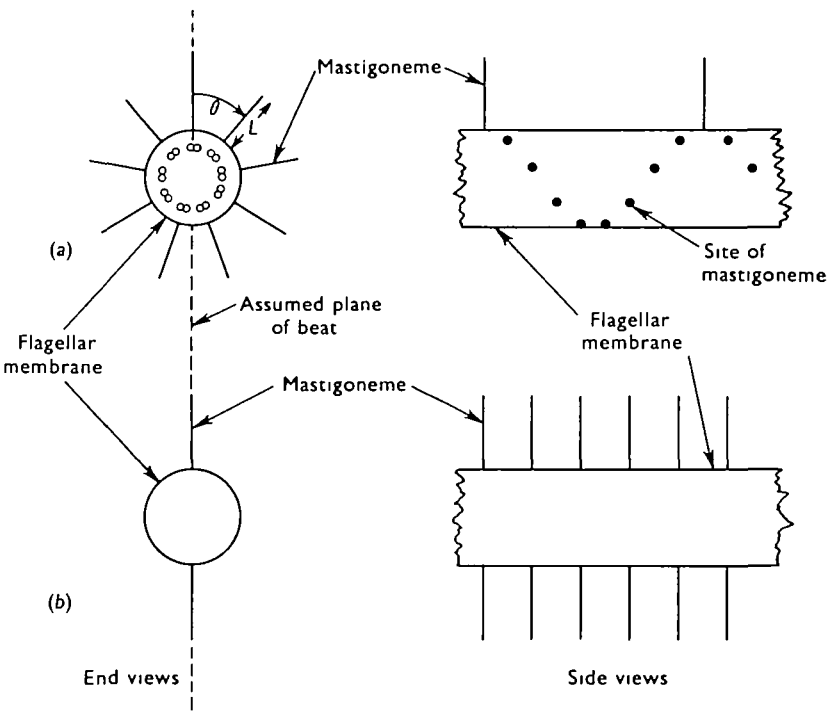

Fig. 3. Idealized arrangement of mastigonemes on the flagella of the organisms described in the text. (*a*) Mastigonemes associated with each peripheral fibre of the axoneme. θ is the angle between the plane of beat and a mastigoneme; L is the length of a mastigoneme. (*b*) Bilateral arrangement of mastigonemes.

patterns of distribution of mastigonemes on flagella have been described; some flagella have a single row of mastigonemes and are referred to as stichoneme flagella, while others are referred to as pantoneme flagella and it is not certain here whether there is a more or less even distribution of mastigonemes around the flagellum or whether they are arranged in two diametrically opposed rows.

Consider a cylinder of unit length bearing t rows of q rod-like projections of equal length L (Fig. 3*a*), and moving with unit velocity perpendicular to its axis in the direction y. Then, for the complete system, we have, approximately

$$C_N = C_N^c + qL \sum_t (C_T^p \cos^2\theta_t + C_N^p \sin^2\theta_t), \tag{16}$$

where the superscripts c, p refer to the cylinder and projections respectively. Similarly, if the cylinder moves with unit velocity parallel to its axis,

$$C_T = C_T^c + qtLC_N^p. \tag{17}$$

In obtaining equations (16) and (17) the influences on the fluid flow around one projection produced by neighbouring projections and the main cylinder have been neglected. Provided the projections are not too close and fluid flow around the system is streamlined, the errors arising from this approximation are not likely to be large.

A PRACTICAL APPLICATION OF THE HYDRODYNAMIC EQUATIONS

The flagellar movement and structure of *Ochromonas malhemensis* and of an unidentified chrysomonad flagellate have been studied with a view to testing the equations derived in the theoretical section. When one of these organisms is swimming freely,

Table 1. *Observed quantities pertaining to flagella and their movement*

Parameter	*Ochromonas malhamensis*	Unidentified chrysomonad
Average flagellar length (μ)	19·8	12·8
No. of mastigonemes per μ on flagellum	16·4	16 6
Average length of mastigonemes (L) (μ)	1·1	0·9
Diameter of mastigonemes (μ)	0·02	0·02
Diameter of flagellum (μ)	0·25	0·25
Average wavelength (λ): basally (μ)	4 0	3·2
at the tip (μ)	9·0	8 9
average (μ)	7·05	6·0
Average amplitude (η): basally (μ)	0·65	0 75
at the tip (μ)	1·25	1·15
average (μ)	0·95	0·95
Average frequency of beat (cyc./sec.)	68·4	57·0
Water velocity (average of several organisms (μ/sec.)	64·5	45·0
Maximum water velocity measured (μ/sec.)	73·0	55·0
Swimming speed (μ/sec.)	55–60	—
Temperature (° C.)	18	20

the flagellum is held out in front of the body and planar waves are propagated distally; the wave motion and the translational movement of the organism are thus in the same direction. The flagellates can also remain stationary on a temporary stalk attached to the substrate and in this condition currents of water are observed to flow about the flagellum. The flagellar activities of organisms of both species in the sessile state and of *Ochromonas* in the swimming condition were examined using stroboscopic and photographic techniques. The results are shown in Table 1. Figures for the form of the flagellar wave were obtained from flash photographs; these indicate that the wavelength of the undulations increases from the base towards the tip. The amplitude of the wave motion also varies along the flagellum. Presumably the purpose of this waveform is to produce food-bearing currents of fluid which will impinge at or near the base of the flagellum, as previously described for *Monas* (Sleigh, 1964). The frequency of beat was measured stroboscopically, and it was possible to confirm using the stroboscope that the flagellar beat was planar and not helical. The velocity of particles in the currents close to the flagellum and the speed of swimming organisms were measured from cinematograph films.

To calculate the surface coefficients of resistance for the flagellum, electron micrographs were obtained to determine the number, size and arrangement of mastigonemes about the flagellar shaft. In micrographs of negatively stained material, where the whole flagella are flattened against the supporting film when they are dried, the flagellar appendages appear to be arranged fairly regularly along the two sides of the flagellum. These mastigonemes may be distributed all around the flagellum, like the hairs on a bottle brush, in rows opposite each of the 9 outer doublets of the 9 plus 2 fibrillar configuration of the axoneme (Fig. 3*a*), or the mastigonemes may be arranged in two rows at opposite sides of the flagellum (Fig. 3*b*). If the mastigonemes are in two rows, the rows must lie in the plane of beat of the flagellum to be fully effective. The only irregularity to be observed in the distribution of the mastigonemes is an apparent clumping of some of the mastigonemes in groups of 2 to 4, especially in the unidentified chrysomonad.

If it is assumed that the mastigonemes are rigid and remain normal to the flagellar surface at all times, then in the 9-row configuration the angle between two adjacent mastigonemes is 40° (Fig. 3*a*). If the flagellum beats in a plane perpendicular to that containing the two central fibres of the flagellum, then one row of mastigonemes will move in this plane. There is some evidence for this plane of beat in certain cilia (Fawcett & Porter, 1954; Bradfield, 1955; Gibbons, 1961), but other cilia can apparently beat in any plane (Okajima, 1953; Parducz, 1954; Sleigh, 1960); no comparable evidence is available for flagellar movement. For the purposes of calculation it will be assumed that for a flagellum with mastigonemes arranged in the 9-row configuration the plane of beat is such that one row of mastigonemes moves in the plane of beating, but no assumptions are made regarding the relative arrangement of the central fibres and the two rows of appendages; indeed, if the 2-row configuration is proved, it should be possible to show the orientation of the central fibres relative to the plane of beat from electron micrographs of sectioned flagella. The assumption of a plane of beat enables us to fix the values for the angle θ for all mastigonemes in each configuration. If the flagellum actually beats in some other plane the differences between the true surface coefficients and those calculated on the basis of the above assumptions will be small for the 9-row configuration but will vary widely for the 2-row pattern. The variation of the ratios C_T/C_N and u/V_w with the angle between the plane of beat and the bilaterally arranged mastigonemes for a flagellum having characteristics similar to those of *Ochromonas* are shown in Fig. 4.

Substitution of average values in equations given earlier allows the calculation of C_T/C_N, u/V_w and hence u (Table 2). The velocity u in equation (9) is that of an isolated flagellum, but will not be greatly different from the velocity of fluid in the immediate neighbourhood of a fixed flagellum, particularly at the low Reynolds numbers involved in the system under consideration. Clearly the value of C_T/C_N must be larger in the 2-row configuration, and this results in a larger value of u for flagella of this type. The finding that the speeds of movement of particles around the flagella of sessile cells and the velocity of swimming cells of *Ochromonas* are very close to the calculated velocities for the 2-row configuration suggests that this is the most likely distribution of mastigonemes. If the mastigonemes are arranged in two rows, but are clumped in groups along these rows, the velocity u will be somewhat lower than where the mastigonemes are distributed uniformly along the rows; values between

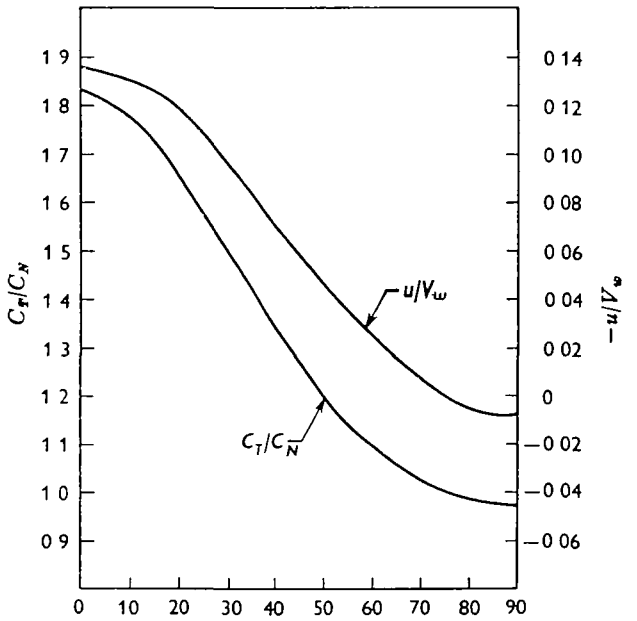

Fig. 4. Variation of C_T/C_N and u/V_w with θ for a bilateral arrangement of mastigonemes. θ is the angle between the plane of beat and the mastigonemes.

Table 2. *Quantities calculated from the observed data*

Quantity	*Ochromonas malhemensis*	Unidentified chrysomonad
Average wave velocity ($V_W = f\lambda$) (μ/sec.)	481	342
ηk	0·85	1·0
9-row configuration		
C_T/C_N	1·23	1·21
u/V_w (sessile organisms)	0·052	0·06
u (sessile organisms) (μ/sec.)	25·1	20·5
u/V_w (swimming organisms)	0·049	—
u (swimming organisms) (μ/sec.)	23·2	—
2-row configuration		
C_T/C_N	1·83	1·80
u/V_w (sessile organisms)	0·136	0·174
u (sessile organisms) (μ/sec.)	65·5	59·5
u/V_w (swimming organisms)	0·126	—
u (swimming organisms) (μ/sec.)	60·6	—

Explanation of symbols—C_T, C_N: surface coefficients of resistance; u: fluid velocity or translatory velocity of organism; f: beat frequency; λ: wavelength of flagellar wave. (For further explanation see text.)

10 and 20% lower would be obtained if the mastigonemes are in groups of three, the actual value depending on whether the members of each group are spread out or lie close together. The velocity of the water current around flagella of the unidentified chrysomonad is rather below the calculated value of u for the 2-row configuration, but not very different from the value that would be expected where the mastigonemes

are clumped, as they appear to be in the electron micrographs; the observed value is certainly higher than the calculated value of u for a 9-row distribution of mastigonemes.

DISCUSSION

The close agreement between the observed and calculated velocities for *Ochromonas* suggests that the theoretical basis for the mathematical analysis is sound, but the assumptions made during the analysis must be borne in mind. Further experiments on a variety of organisms bearing hispid flagella need to be performed to estimate the magnitude of the error incurred by these assumptions.

The agreement between the velocities makes it more certain that, during movement, the mastigonemes remain perpendicular to the flagellar surface, a situation which has been assumed for the purposes of calculation but which cannot be directly verified at present since the size of the mastigonemes is below the resolving power of the light microscope. The failure of the hispid flagella of certain organisms (e.g. *Euglena*) to exhibit reversal of the propulsive force may be because the lateral hairs are wrapped around the flagellum during movement, or because they are much more flexible. Alternatively, the mastigonemes may be normal to the flagellar surface but may be of insufficient length to render the ratio C_T/C_N greater than unity [the condition for this inequality can be derived in any particular case from equations (16) and (17); see also Holwill (1966)]. The hairs on the flagellum of *Euglena* are up to 4 μ long and are much thinner than the mastigonemes of *Ochromonas* (Pitelka, 1963). The dimensions of the euglenoid hairs are such that reversal would occur if they remained normal to the flagellar surface during movement and if they were held in a suitable position during movement; it appears that they have a different function from the mastigonemes described earlier and should be referred to by a different name.

It is interesting to note that the graph of u^2/P against ηk (Fig. 2) has a broad maximum in the region $\eta k = 1$, and has a similar form to the comparable plot for smooth flagella executing sinusoidal and helical waves (Holwill & Burge, 1963). The values of ηk for the flagella examined here are close to unity (Table 2); the flagella appear therefore to be operating close to their maximum propulsive efficiency.

SUMMARY

Equations are derived for the propulsive velocities and power dissipation of undulating hispid flagella. The observed rates of movement of water around the flagella of two chrysomonad flagellates and the translational speed of *Ochromonas malhamensis* agree closely with values calculated if it is assumed that the flagellar mastigonemes remain perpendicular to the flagellar surface and that these mastigonemes lie in two diametrically opposed rows situated in the plane of the flagellar wave.

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